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Department of Biological Sciences, Wye College (University of London),
Ashford, Kent, England

Field and laboratory studies on the activities of two species of tropical earthworms

By David S. Madge

With 12 Figures

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1. DISTRIBUTION IN THE FIELD

1.1. Surface casts

The presence of earthworm casts, often very numerous during the rainy season, is one of the most interesting features of grassland soils in southern Nigeria. Two main types of casts are easily recognized: one type is found mainly in shaded grassland, the other mainly in open grassland. The wormcasts in the shade are funnel-shaped, varying from about 2.5 to 8 cm high and 1.0 to 2 cm wide (Fig. 1); those in the open consist of small,

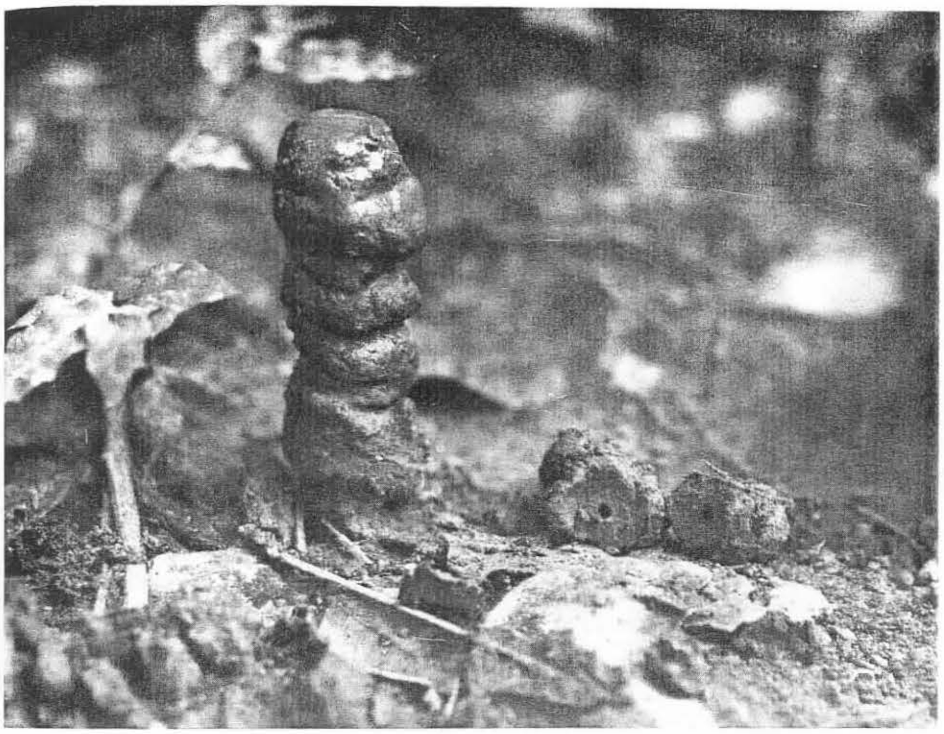

Fig. 1. Cast of *Hyperiodrilus africanus* BEDDARD. Note — worm hole in broken cast on right.

loose granular mounds, 3—5 cm in base diameter and of variable height, but generally under 3 cm (Fig. 2). The second type of wormcasts resemble mounds of soil thrown up by ants in these same vicinity. However, the wormcasts are easily distinguished from ant mounds by their pellet-like appearance, softer texture and by lack of arthropod remains around the base of the mounds.

Preliminary observations were made at intervals during May, June and September 1964 on exposed and shaded grassland sites on the University of Ibadan campus in Nigeria. Areas which received both sunlight and shade were also noted: about one-quarter of the total grassland area studied was exposed at intervals to both sunshine and shade. Quadrats 1 m^2 were marked out in June 1964 in the different grassland sites and the total number of the two different types of earthworm casts in these plots recorded. The results obtained (Table 1) clearly show that the funnel-shaped casts were confined to shaded grassland and the mound-shaped casts were mainly fou

Fewer casts, mainly of the mound type, were found in the area receiving both sunshine and shade. A number of mound-shaped casts in the open may have been missed, since they were sometimes partly hidden in the grass or were lost owing to rain and wind.

1.2. Earthworms

After counting the surface casts in the three areas of grassland (Table 1), the earthworms were recovered from the plots (method later), identified and counted. Two closely-related species were identified, both belonging to the family Eudrilidae (sub-family Eudrilinae), which is confined to tropical and sub-tropical Africa (STEPHENSON 1930; OMODEO 1958). The species in the shade, producing funnel-shaped casts, was *Hyperiodrilus*

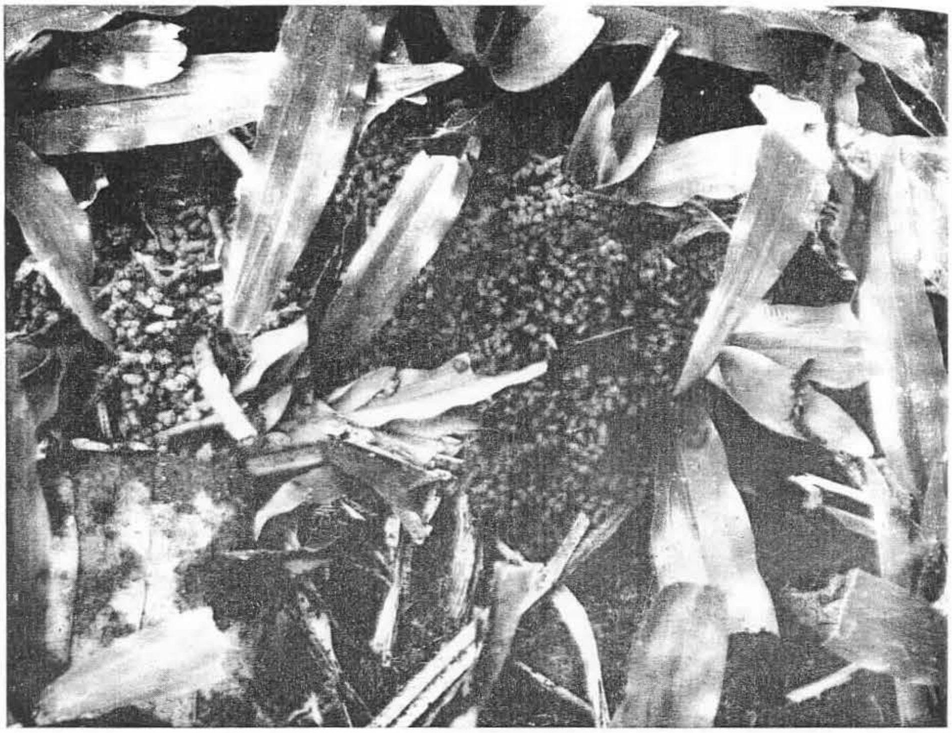

Fig. 2. Cast of *Eudrilus eugeniae* (KINBERG). Dorsal view.

Table 1. Type and average number of earthworm casts on grassland at Ibadan, Nigeria (range in brackets)

Site	Number of plots (1 m² each)	Type of casting	
		Mound	Funnel
Open grassland	14	23 (12—29)	0 (1—0)
Open/shaded grassland	9	9 (3—13)	2 (0—6)
Shaded grassland	19	3 (1—4)	31 (22—46)

africanus BEDDARD, a species found only in certain regions of West Africa and abundant in southern Nigeria; the species in the open, producing mounds, was *Eudrilus eugeniae* (KINBERG), which is more widely distributed in West Africa. Both these species are apparently very plentiful in the coastal regions of West Africa (SIMS, pers. comm.). A miscellaneous collection of other earthworms, consisting of 8—17% of the total population in both sites, were not identified.

1.3. Surface activity

During the rainy season both species produce surface casts continually. Owing to heavy rainfall these casts are gradually washed away, leaving small, irregular heaps of soil. Casts are not produced during the dry season, although *Hyperiodrilus* continues casting for several weeks in damp areas in forests after the start of the dry season. The casting activity of *Hyperiodrilus* in shaded grassland was investigated by marking different plots 1 m² and collecting casts (a) daily, (b) at 7-day intervals, and (c) at 6-weekly intervals from different plots, the experiments lasting from mid-April to the end of June 1964. The casts were removed at ground level with a sharp knife, oven dried at 105 °C for 24 hours, then counted and weighed.

Casts of *Eudrilus* were collected daily in open grassland from quadrats 1 m². Attempts to collect other casts at weekly intervals or longer were unsuccessful because the loose material disappeared after rainfall or, when dry, became dispersed by wind. The approximate size of both kinds of casts was also measured.

1.3.1. *Weight of casts*

The results are summarized in Table 2. Both species voided 3.2 gm of surface casts each day. The amount of surface activity of *Hyperiodrilus* per day for 5 weeks remained constant. *Hyperiodrilus* produced casts weighing on average 9.2 gm per week, and after 6 weeks only 20.8 gm of casts remained. Hence, over 80% of wormcasts are washed away by rainfall during part of the rainy season. Therefore, for each species, assuming an average of about 30 worms per 1 m² (see below), each worm voiding 3.2 gm of surface casts daily for the 6 months of the wet season, about 70 tons of surface casts are produced/acre/year.

Table 2. Average weight and size of earthworm casts collected on grassland soil (S. D. in brackets)

Earthworm species	Collecting periods	Total number of collecting periods	Total number of casts weighed	Average weight of casts (gm)	Average dimensions of casts: height × base diam. (cm)
Eudrilus eugeniae	daily	18	476	3.15 (0.45)	2.6 × 4.2
Hyperiodrilus africanus	daily	35	979	3.17 (0.36)	2.8 × 0.9
	weekly	6	314	9.18 (0.77)	6.6 × 1.3
	6-weeks	4	84	20.74 (1.98)	8.1 × 1.7

1.3.2. *Number of casts*

Grassland plots with casts of each species were treated with diluted formalin to expel the earthworms, the worms collected and preserved in formalin, and then identified and counted. The ratio of *Eudrilus:* casts in open grassland was 0.9 : 1, and the ratio of *Hyperiodrilus:* casts in shaded grassland was 1 : 1.2. Worms from observations on wormcast activity lasting 5 weeks for *Hyperiodrilus* and lasting $2^1/_2$ weeks for *Eudrilus* were also recovered from different plots at the end of the experiments and compared with the average number of casts in these plots. The ratio worms: casts for each species was almost 1 : 1. Therefore, it appears that these worms only produce one cast per individual.

1.3.3. *Diurnal activity*

Surface casts are usually produced during night-time, although worms were sometimes seen either casting during the day following rainfall when the humidity was high, or on dull, humid days. Both species were never seen on the soil surface. Unlike some lumbricids in temperate regions, the Nigerian earthworms rarely emerged from their burrows following rainfall. However, one large species, *Millsonia nigra* (COGNETTI), was sometimes seen on the soil surface after rain.

1.4. Rainfall and casting activity

Observations were made during the dry season of 1965—66 until the wet season of 1966. Routine sampling was stopped on 17. 11. 1965, when earthworms were no longer recovered. By then the soil surface was very dry, the rains of 1965 having ended 15 days earlier, and surface casting had ceased 2—3 weeks previously.

Between 1. 11. 1965 and 1. 3. 1966, there was moderate-heavy rainfall on four separate occasions, each lasting $^3/_4$ — $1^1/_4$ hours. A pit of about 50 cm² and 80—90 cm deep was dug in both open and shaded grassland soil, and soil samples taken at different depths on 5 separate occasions during this period. The soil samples were first examined for earthworms, then the moisture content of the samples found by drying the soil in an oven at 105 °C for 24 hours.

During November-February casting activity was not observed on either site. Three large worms were collected during the first sampling occasion (16. 2. 1966) at a depth of about 10 cm in shaded grassland soil a week after rainfall (soil moisture content 6.3 % oven dry weight). Two further mature worms were collected during the fourth collection (13. 3. 1966) at 25 cm depth, with a soil moisture content of 11.3 %. The worms recovered on both occasions were turgid and slow-moving, but became more active when left in water.

Owing to the porous nature of the soil in both sites, after rainfall the soil became uniformly moist to a depth of at least 40 cm, and remained fairly moist even 5—7 days afterwards, except for the top 5 cm which tended to dry out. The soil of open grassland was slightly drier than that of shaded grassland. For example, the soil moisture content at different depths averaged 6.8 and 7.3 % a week after rainfall for open and shaded grassland respectively (16. 2. 1966). There was no further rainfall for three weeks, the average soil moisture decreasing to 3.2 and 5.6 % respectively, but soil moisture increased below 20 cm.

Between 15.—30. 3. 1966 there were 3 further periods of medium heavy rainfall, each lasting for about 1 hour. The soil remained moist throughout this period, the moisture penetrating to a depth of at least 50 cm. The average moisture content of the soil was 14.1 % for open grassland and 14.4 % for shaded grassland (field capacity 15.4 and 15.8 % respectively); it remained at this high level thereafter.

By 20. 3. 1966 a few medium-sized surface casts appeared in the open grassland, but hyperiodrilid casts were not yet seen in the shade.By 5. 4. 1966 heavy rain fell several more times: Eudrilid casts became common and hyperiodrilid casts then became evident. Hence, there is a time-lag of 2—3 weeks between the casting activity of the two species. Thereafter they both casted continuously throughout the remainder of the wet season, except for short, rainless periods when the surface activity of both species temporarily decreased.

Other attempts were made to investigate differences between casting activities of the two species. Grassland (open and shaded) plots known to contain large numbers of earthworms were watered daily from the start of the dry 1965—66 season for 2 months, corresponding to an average wet season daily rainfall 5.5 *l* (1.2 gals/1 m²). Casting on watered plots continued for 2—3 weeks longer than on control plots, then soon diminished and stopped. The topsoil in the open quickly dried, even when watered, but the soil remained damp below.

The experiment was repeated from late February to late March 1966, that is, about one month preceding the onset of the rainy season. Casting activity was not noted until late March, and casts appeared simultaneously on unwatered (controls) plots. However, by then there were 4—5 times more casts in the watered plots compared with the unwatered ones, but by mid-April differences were less obvious. Temperature records

Table 3. Average soil temperature (range in brackets) at a depth of 2.5 cm in shaded or open grassland. Average readings for 10 consecutive days given (March—April 1966)

Plots	Temperature °C		
	0800 hrs.	1300 hrs.	1900 hrs.
Shade, watered	24.7 (23.4—25.5)	27.6 (27.0—30.3)	26.4 (24.8—27.2)
Shade, unwatered	26.7 (26.3—27.5)	29.5 (29.6—30.1)	30.1 (29.4—31.0)
Open, watered	27.1 (26.3—28.4)	37.7 (35.6—38.4)	32.0 (31.0—33.2)
Open, unwatered	28.5 (28.0—29.5)	42.2 (38.2—46.5)	34.9 (32.5—36.1)

2.5 cm deep in experimental and control plots were taken at 0800, 1300 and 1900 hours for 10 consecutive days (Table 3). The temperature of the watered plots was 2.5 °C cooler than that of the controls, depending on the time of day.

The results of the second experiment on casting activity were unexpected, for it was anticipated that worms in soil with artificial rainfall would have resumed surface casting before the controls. However, the activity of earthworms probably depends upon the balance between both optimal moisture and optimal temperature, and the temperature may still have been too high for surface casting. The appreciably greater number of casts on the watered plots suggest that worms probably migrated from adjacent areas deep in the soil profile, which presumably remained moist throughout the year. The lateral seepage of water to adjacent, unwatered plots was small.

2. SEASONAL ACTIVITY IN THE FIELD

2.1. Methods

Investigations in the field were made only in shaded grassland. Worms were brought to the surface by treating six random plots, each 1 m² each, week during the wet season with diluted formalin (Raw 1959; Madge 1965a). The worms that emerged were immediately dropped into 5 % formalin, and later identified and weighed (they lost about 20 % of their fresh weight in formalin).

Preliminary investigations during the previous wet season showed marked differences in the colour and shape of the two main species of worms preserved in formalin. First, *Hyperiodrilus* rapidly turned uniformly grey and opaque and tended to contract, whereas *Eudrilus* remained irridescent and became extended. Secondly, the clitellum of the first species often turned dark grey in the preservative; that of the second turned brown with time. These consistent differences — especially the first — proved a fairly reliable means of readily identifying the two species, including the immature forms, when it was otherwise difficult to do so.

Plots were periodically sampled during the dry season of November 1964 to March 1965, and always following intermittent rain, but worms were not found, nor surface casts observed. Towards the start of the following wet season (April 1965) plots were sampled regularly at weekly intervals at the same time of day, and sampling repeated until the start of the following dry season (November 1965) when surface casting activity caesed. As far as possible, different quadrats in shaded grassland were sampled on each occasion.

2.2. Results

Earthworms were recovered from April 24th, 1965 until November 17th, 1965, that is, for 28 weeks. The recovery of the worms coincided with surface casting activity. During that time, a total of 5,400 earthworms were collected. Of that total, 71 % were *Hyperiodrilus* and 11 % were *Eudrilus;* the remainder consisted of unidentified worms, including a few large specimens of *Millsonia nigra* (Cognetti) (fam. Octachaetidae). An average of 33 individuals of *Hyperiodrilus* were recovered per plot 1 m² during the whole sampling period. Figure 3 shows the general fluctuations in the number and weight of worms each week, and also includes daily rainfall and weekly average soil temperature, 2.5 cm deep. Three peak numbers of worms were obtained, the first in May (weeks 1—4), the second in July-August (weeks 10—15) and the third during September—October (weeks 19—24). The rainfall was heaviest in July and least in late October and November.

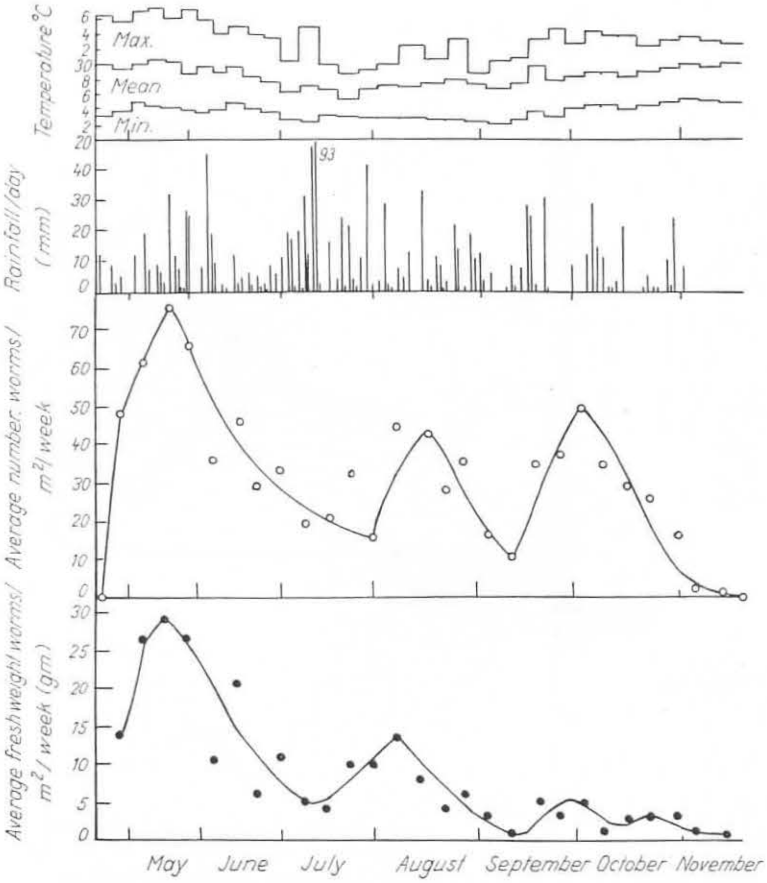

Fig. 3. Population fluctuation (numbers and weight) of *Hyperiodrilus africanus* during the wet season in 1965 in shaded grassland soil at Ibadan, Nigeria. Daily rainfall and 7-day average soil temperature (2.5 cm depth) also shown.

The temperature was warmest during May and November (average 30 °C) and coolest during August and September (average 27 °C). Generally, the total fresh weight of the worms fluctuated with the total number of earthworms. However, the weight decreased progressively at each successive peak number owing to a decrease in adult numbers and an increase in immature forms as the wet season progressed.

Figure 4 illustrates the average number of worms collected each week during most of the rainy season. For convenience, the worms have been graded into three categories: large (over 6 cm), medium (3—6 cm) and small (less than 3 cm). At the start of the wet season (weeks 1—6), only large and medium-sized worms were recovered. The numbers of large worms gradually declined until early August (week 12), but there was a corresponding increase in numbers of small worms, which reached a peak by the 9th—11th week. By the end of August (week 15) the majority of the worms were medium-sized, and found in greater numbers compared with the first early peak, and there were only few large or small worms. The number of adults then rose again to a new peak by late September (week 19), but only about half the total numbers were recovered with the

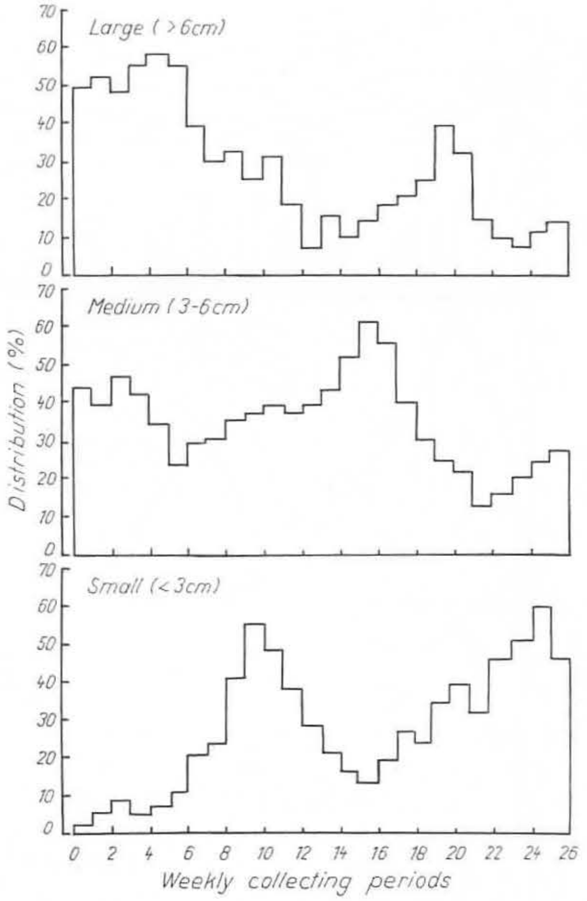

Fig. 4. Population fluctuation of hyperiodrilids, based on three group-sizes, during the rainy season in 1965.

previous early peak collected at the onset of the wet season. Towards the end of the wet season (week 24) the samples contained mainly small worms again.

The low numbers of small worms collected at the start of the wet season were unexpected, for many were found at the end of the wet season. Hence, this result suggests that the worms did not aestivate during the dry season, but that their life-history was continued deeper down in the moist soil during that period. This hypothesis will be substantiated later (3.1.), for it has been shown that young worms hatched in moist soil under artificial conditions during late February, that is, corresponding to the middle of the dry season and were reaching maturity by April, that is, at the start of the following wet season under natural conditions.

Thus, the life-history may be tentatively summarised as follows. The first generation is produced during the dry season, the worms developing into mature forms early in the wet season. Cocoons are then laid and juveniles develop during the middle of the wet season to produce the second generation. A third generation then develops from the end of the wet season to mature once again during the dry season.

Figure 5 gives the relationship between the fresh weight of *Hyperiodrilus* and their length. The smallest worms recovered were about 0.8 cm long and less than 1 mm in diameter across the clitellum, and weighed about 0.15 gm; the largest rarely exceeded 10 cm in length and 4 mm in width, and weighed about 7 gm, although a few recovered which were 10—11 cm long and about 5 mm in width, and weighing about 8.5 gm. Most of the mature forms averaged about 8 cm long and 3.5 mm in diameter. Measurements of eudrilids were not made, but observations suggested that this species was slightly larger than the first.

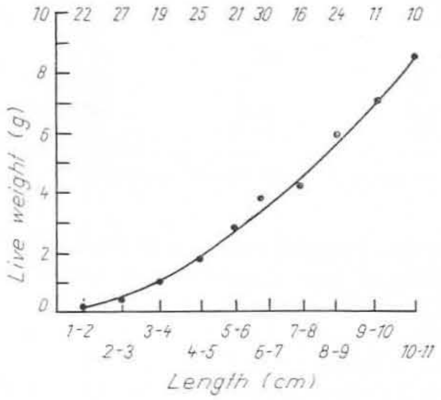

Fig. 5. Relationship between fresh weight of hyperiodrilids and length. Number of worms measured also indicated.

2.3. Analysis of the soil

2.3.1. *Soil profile*

A profile 100 cm deep was dug in both shaded and open grassland and the main features noted. Both profiles were essentially similar, so only a generalized description is given. The topsoil, 10—15 cm deep, was a coarse, brown, crumbly and porous texture, with grass roots (mainly in the open grassland) in the upper 5 cm. Below the topsoil, the profile changed to a brownish sandy-loamy soil, followed by a stony layer at a depth of 35—40 cm. Below the gravelly horizon, the soil changed abruptly to a reddish, silty clay, with few stones, and crumbly quartz veins, of unknown depth.

2.3.2. *Mechanical analysis of the soil profile*

Soil samples were taken at intervals down the soil profile, transferred to labelled, sealed containers and air-dried in the laboratory. Weighed samples of soil (100 gm. each) were dispersed in 0.5 N sodium hexametaphosphate, passed through a 70 IMM sieve, washed and dried in an oven at 105 °C for 24 hours, the stones and concretions larger than 2 mm in diameter removed, and the quantity of coarse sand left found by weighing. The silt and clay fractions of each sample were determined by Bouyoucos' hydrometer method (Bouyoucos 1936), and the quantity of fine sand obtained by Piper's decantation method (Piper 1942). Earthworm casts, and ant mounds (open site only) were likewise treated. The *p*H of the different samples was also taken with a Beckman (model 72) *p*H meter.

Table 4 summarises the results. Separate data of the samples from each site or from each species of earthworm are not given since the results were fairly similar. However, the average amount of fine sand and silt from the soil profile in the shade was 5—10% higher than from in the open, and the amount of coarse sand from the profile in the open correspondingly lower. This difference was also reflected in the mechanical analysis of the worm casts: *Hyperiodrilus* in shaded grassland had a slightly higher fine sand and silt fraction, but a lower coarse sand fraction, compared with *Eudrilus* in open grassland.

Table 4. Mechanical analysis of the soil profile from grassland, including surface casts of earthworms and ant mounds (expressed as % of total fine earth)

Depth (cm)	Coarse sand	Fine sand	Silt	Clay	Total	*p*H
Earthworm casts	14.4	42.5	26.5	16.5	99.9	7.5
Ant mounds	79.3	13.9	3.5	2.5	99.2	7.5
0—5	47.9	16.6	18.5	15.5	98.5	7.4
5—12	67.4	8.0	11.5	14.0	100.9	7.1
12—20	70.8	6.8	11.0	13.0	101.6	6.9
20—30	69.7	6.7	13.0	11.0	100.4	6.5
30—40	63.0	10.7	15.0	11.0	99.7	6.4
40—50	56.4	15.1	18.5	11.5	101.5	6.1
50—75	42.4	24.1	23.0	11.0	100.5	5.9
75—100	36.0	26.0	25.5	14.0	101.5	5.8

N.B. A stony layer was noted at about 35—40 cm depth.

The top soil layer (0—5 cm) of each profile consisted of approximately 50% coarse sand and the remainder of approximately equal quantities of fine sand, silt and clay. Immediately below, the coarse sand increased to over 2/3 of the total amount, while the fine sand and silt decreased. Between 40—50 cm the fine sand and silt increased, and continued increasing deeper down the profile, while the coarse sand and clay content decreased. At a depth of 100 cm, about 1/3 of the composition of the soil was coarse sand; 1/2 of it was fine sand and silt, and the clay increased slightly again to about 1/7 of the total.

The mechanical composition of the earthworm casts and ant mounds showed interesting differences compared with that of the soil profile. There was considerably less coarse sand in the earthworm casts compared with any depth of soil beneath, and appreciably more fine sand. The amount of silt and clay in the casts corresponded closely to the amount in the soil at a depth of 100 cm. The amount of silt and clay at 0—5 cm depth was rather lower than the amounts in the casts. Thus, it appears that the worms are ejecting soil brought up from considerable depths — possibly over 100 cm — below the surface. The earthworms' contribution to the formation of the surface soil is obvious.

The mechanical composition of ant mounds differed considerably from that of earthworm casts. Over 3/4 of the total soil fraction consisted of coarse sand, and most of the remainder was fine sand. Thus, the activity of earthworms in modifying the topsoil is much more important than that of ants.

The *p*H of the soil profile was slightly alkaline in the topsoil, gradually decreasing to an acid reaction lower down the profile. The *p*H of the wormcasts and ant mounds was close to that of the topsoil.

2.3.3. *Organic matter content*

The organic matter in the topsoil, earthworm casts and ant mounds in the two areas was detemined by the Walkley and Black method (Walkley and Black 1934; Walkley 1935). Ten samples of soil, 5 cm × 5 cm, were taken at random from each site, and each sample triplicated. Determinations were also made on 10 samples from surface casts of each species of earthworm, and on 7 samples from ant mounds in the open, and each sample also triplicated.

The analysis showed (Table 5) that the difference in organic matter in the soil in both areas was not statistically significant. The organic matter of the two types of earthworm casts was also similar, and each over 3 times higher than that of the topsoil. The organic matter of *Hyperiodrilus* casts was slightly, but not significantly, higher than that of *Eudrilus* casts. The organic matter of the ant mounds was 4 times lower than that of the topsoil and about 13 times lower than that of the earthworm casts.

Table 5. Organic matter content of topsoil, earthworm casts and ant mounds from grassland (June and October 1965)

Sample	% organic C (uncorrected)	% organic C (corrected)	% organic matter
(1) Shaded grassland	0.79	1.07	1.84
(2) Hyperiodrilid casts	2.59	3.50	6.04
(3) Open grassland	0.64	0.87	1.50
(4) Eudrilid casts	1.97	2.66	5.59
(5) Ant mounds	0.17	0.23	0.39

1/3 and 2/4 NS; 1/5 and 3/5 $P < 0.001$; 1/2 and 3/4 $P < 0.001$; 2/5 and 4/5 $P < 0.001$.

3. ACTIVITY UNDER LABORATORY CONDITIONS

Although individuals of both species of earthworm were used separately in some laboratory experiments, no marked differences in behaviour were generally detected. Therefore, combined results are usually presented.

3.1. Activity in moist soil

One hundred medium-large worms of *Hyperiodrilus* (only) were placed in a wooden box (50 cm high and 60 cm^2) filled with topsoil to within 10 cm from the rim. The box was left undisturbed in a shaded corner of an open verandah, and watered regularly every third day in amounts corresponding to an average daily rainfall (5.5 *l*/1 m^2), during which time the water-content of the soil fell from about 34% (% dry weight basis) to about 19%. Before wetting the soil, the total number of surface casts was counted on each occasion, and the casts then ground to a powder and spread over the soil surface. The temperature of the soil, 2.5 cm below the surface, was taken at about 1 p. m. daily (preliminary records showed that the temperature at that time averaged morning and evening readings). The experiment was started at the end of the wet season, on November 1st 1965, and ended at the start of the following wet season, on April 15th 1966.

The results are summarised in Fig. 6. Throughout the experiment the temperature remained fairly constant, averaging 29 °C (range 27.9—30.4 °C), falling slightly below average from mid-December to mid-January and rising slightly above average from mid-February to mid-March.

The total number of surface casts fell progressively from the start of the experiment, remained low from mid-January to mid-February, and then rose abruptly and continued rising until, by the end of the experiment, the number of casts exceeded those at the start. Since individual worms produce only one cast each (1.3.2.), it is reasonable to assume that the immature worms at the start of the experiment in November reached maturity in under two months, then laid cocoons that hatched in about 4—5 weeks, in mid-February. Two further observations supported this conclusion. First, the size of the casts were appreciably smaller when the number of casts began to increase in March: secondly, a number of casting worms were measured during that period, and the majority found to be less than 1 cm long. Also, the dimensions of the worm casts at the end of the experiment were approximately similar to those at the start, indicating that the worms had matured. The decrease in number of wormcasts during the first half of the experiment was more likely due to a mortality among mature worms than to a decrease in casting activity, since both temperature and moisture remained fairly constant throughout the experiment. Furthermore, the increase in size of the wormcasts from March onwards was progressive, and there was little or no overlap in cast size when the small casts first appeared.

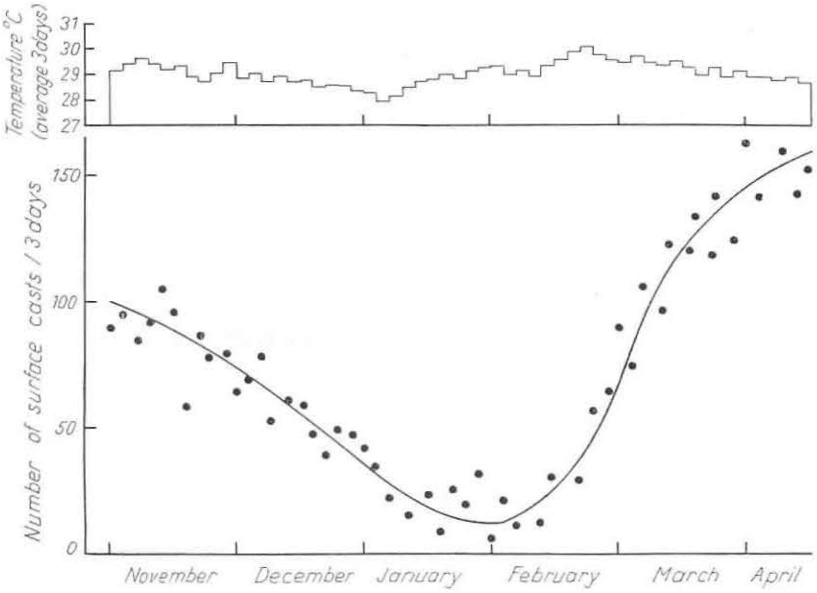

Fig. 6. Surface casting activity of earthworms in moist soil. Temperature fluctuations also given.

Hence, it is concluded that worms reached maturity during November, eventually laid cocoons which hatched at the end of February, the immature worms reaching maturity during April, that is, at the start of the wet season. These results are correlated with field observations, for only medium-large worms were recovered in early May (Fig. 4).

3.2. Experiments in a soil moisture gradient

Surface soil and wormcasts were taken from the field (pH 7.4), left to dry in an air-conditioned room at about 25 °C and 45—55 % R.H. for a week, then crumbled and mixed. Different amounts of water were thoroughly mixed with six equal samples of soil, and the soil then packed in equal proportions into a wooden box measuring 120 cm long, 16 cm wide and 20 cm deep, leaving a gap approximately 5 cm on top. Each soil sample was separated from adjacent samples by a thin vertical layer of dry soil. Batches of 100 worms of mixed sizes of each species were evenly distributed over the whole soil surface and the box covered with a lid. After 48 hours, the number of surface casts on each soil sector was counted, the soil removed and the number of worms found in each sector. The experiment was repeated 5 times with different batches of worms, using approximately the same soil moisture content. Estimations of soil moisture contents before and after each experiment showed that soil mixing in adjacent sectors was small, with overall differences of about 10 % for wetter soils and less than 4 % for drier soils.

Figure 7 summarises the results obtained. About two-thirds of the total number of worms of both species aggregated in soil containing an average of 12.5—17.2 % moisture contents ($P < 0.001$). Generally, soils containing 1—4 % moisture and 22.5 % moisture were avoided; less than one fifth of the total number of worms were collected from soil having an 8 % moisture content. The distribution of worms of different size-groups and soil moisture content was not related. Some worms placed on the drier soils were unable to burrow, and eventually died of desiccation.

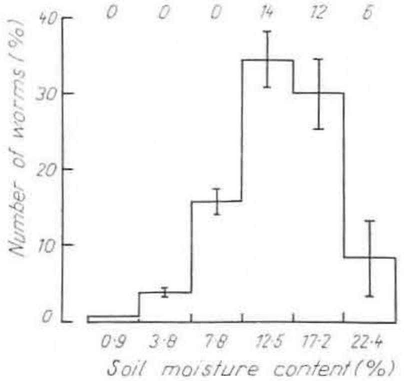

Fig. 7. Effect of soil moisture gradient on the distribution of earthworms after 48 hrs. at 25 °C (S. D. as vertical lines). Number of surface casts also shown.

About one-third of the total number of worms aggregating in soils with 12.5—17.2% moisture contents produced surface casts. Casts were not observed on the surface of soils containing about 1—8% moisture content, and only few noted on soil with 22.5% moisture content.

A control experiment was made by evenly distributing a batch of 90 worms of each species on the soil surface with a uniform moisture content of 13.5%. After 48 hours the worms remained evenly scattered in the soil and some casted over the entire soil surface.

3.3. Earthworm casting and soil moisture

One hundred worms of mixed sizes of each species were placed separately in two wooden boxes (45 cm deep × 60 cm²) filled with surface soil and left in an open shaded verandah. The temperature of the soil 1 cm deep varied from 24.5—30 °C (mean: 26.5 °C). The soil was thoroughly watered (field capacity: 34.3% oven dry weight), the number of surface casts voided on the surface counted at 0800 hrs. each morning, and samples of surface soil then taken for soil moisture determinations. After 5 days surface casting stopped; on the following day the soil was watered again, and the procedure repeated three times.

Figure 8 summarises the results. When the soil moisture averaged 31.8% about 50% of the total number of worms casted, when it averaged 28 and 18.5% about 80 and 70% casted respectively, and when it fell to 8.5% very few casted. Hence, a soil moisture content of about 23.3% appeared to be the optimum for surface casting. This optimum is unexpectedly high, for in a gradient of soil with different moisture contents (see above) worms aggregated mainly in soils with an average moisture content of about 15%.

3.4. Immersion

Two batches of 15 medium-sized worms of each species were placed in glass containers with fine topsoil, 5 cm deep, overlaid with aerated tap water 15 cm deep. The experiments were made in an air-conditioned room at about 25 °C, but the temperature varied from 22—30 °C on two separate occasions for 2—3 days owing to electricity failure. The worms were removed from the containers and inspected periodically for 9 weeks. During that period, the majority of the individuals survived, but little body growth was apparent. The worms usually remained buried in the mud, although they infrequently emerged for short periods to move along the surface of the mud. In another experiment, two

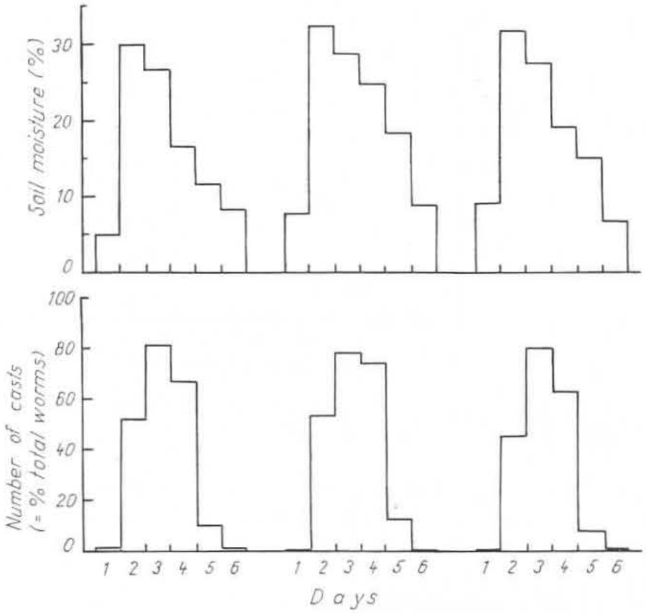

Fig. 8. Effect of soil moisture content on casting activity of earthworms, at 25 °C. Average of three replicates given.

batches of 10 individuals were kept in aerated tap water without soil at about 25 °C. The worms became emaciated after 1—3 weeks, and most of them died by the end of 4 weeks.

3.5. Behaviour in different sand fractions

Four plastic boxes, each measuring 18 cm × 18 cm × 6 cm, were filled to within 1—2 cm from the top with four different sand fractions, each fraction occupying one quarter of the total area of each box. The sand fractions, obtained by sieving through a set of standard brass sieves, had the following diameters: 1.0 mm, 0.5 mm, 0.25 mm and 0.10 mm. The arrangement of the different sand fractions was varied in each box. The

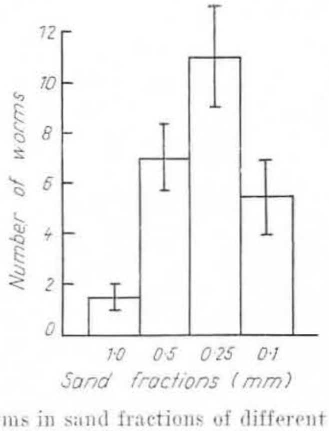

Fig. 9. Distribution of earthworms in sand fractions of different sizes, at 25 °C. Average of four replicates shown (S.D. as vertical lines). Number of surface casts also shown.

sand was thoroughly moistened and four batches of 25 worms of mixed sizes of each species put into each box, where they soon burrowed into the sand. The boxes were covered and left undisturbed in the dark for 48 hrs. at about 25 °C. The sand was then removed, and the number of worms in each of the four different sand fractions counted and measured.

The results, given in Fig. 9, showed that the worms had a pronounced bias for sand with particles 0.25 mm in diameter ($P < 0.001$). They markedly avoided particles 1.0 mm in diameter and remained fairly equally distributed in particles 0.5 and 0.10 mm in diameter (results not statistically significant). There was no relationship between different size-groups of worms and sand of different particle-size. Some surface casting was noted on both sand particles 0.25 and 0.10 mm in diameter, but casts were not produced over the other sand fractions.

3.6. Diapause

Six batches of 30 worms of mixed sizes of each species were put into different wooden boxes filled with surface soil, the soil thoroughly watered for several days (field capacity: 34.5% oven dry weight) and the boxes then loosely covered. The boxes were left undisturbed in a shaded verandah where the temperature averaged 24.5 °C (range 22—29 °C). After 5—6 days the worms stopped casting. After 1, 2, 4, 6 and 8 weeks the soil, each containing a batch of one species, was carefully examined, the worms removed, dropped into petri dishes with water and observed at intervals.

The worms in the experiments lasting for either 1 or 2 weeks gathered at the bottom of the containers, which became lined with hardened earthworm burrows. Most of the worms were knotted and partly shrivelled, but became active when disturbed. In water, they became turgid and active. Earthen capsules or compact mucus secretions were not found. The soil moisture content in the vicinity of the worms was approximately 6% of its oven dry weight. From 4 to 8 weeks in unwatered soil the worms of both species became shrivelled, usually extended and uniformly opaque, and were more evenly scattered in the soil at the bottom of the box. When placed in water, they partly swelled but failed to revive, and some became putrified. The soil moisture content in their vicinity varied between 1.7—5.4% (oven dry weight). It thus appears that the two species of worms, unlike some species in temperate soils, do not diapause. These results were correlated with numerous field observations: earthworms in capsules were never found in soil during the dry season down to a depth of 100—120 cm, where the soil moisture was usually below 5%.

3.7. Effect of desiccation

Medium-sized worms were recovered from the field by digging, washed in tap water and left in plastic containers lined with moist blotting paper for 3—4 days at about 25 °C to clear the gut. Five batches of 5 worms of each species were then weighed on a beam balance (accurate to 0.05 mg), transfered to 500 *ml* beakers covered by fine nylon netting, and the containers left inverted inside large desiccators, with silica gel as the drying agent. The containers were periodically removed from the desiccators during the next 6 hours, the worms quickly weighed and replaced in dry air in unused desiccators. The experiment was repeated 5 times with different batches of worms. The water content of fresh worms was also found by drying them in an oven at 105 °C for 24 hours.

Preliminary experiments using single individuals of each species in dry air showed that after a worm had partly shrunk it became moribund and failed to revive, even when subsequently left in water. This moribund state was thus considered as being a good indication of its mortality in dry air, this criterion being subsequently used for the detailed experiments.

Figure 10 summarises the results of the experiments. Generally, *Hyperiodrilus* lost about 10% more water and died $^3/_4$-hour sooner in dry air at 25 °C compared with *Eudrilus*. There was a 50% mortality after 2 hours with *Hyperiodrilus* and after 3 hours with *Eudrilus;* during this time individuals lost an average of 45.0% and 43.3% of their original body weight respectively. There was a 100% mortality after 6 hours with *Hyperiodrilus* and after about $7^1/_4$ hours (by extrapolation) with *Eudrilus*, the worms losing 69.4 and 62.3% of their original body weight respectively. The water content of fresh worms (oven dry weight basis) averaged 88.4 and 83.8% respectively.

3.8. Experiments in a soil temperature gradient

The apparatus consisted of an insulated copper trough, 80 cm long, 6 cm wide and 4 cm deep, embedded in two insulated boxes at either end. One box was filled with hot water and the other box with crushed ice and salt, giving a temperature gradient of 40—13 °C (± 2 °C) along the chamber (this apparatus is fully described in MADGE 1965b). The copper through was filled to within 1 cm from the top with surface soil, with a moisture content of about 12.5% (oven dry weight). The apparatus was covered with a double-walled glass lid, and the temperature of the soil taken every half hour with mercury thermometers inserted trough 10 holes equally spaced apart in the glas lid. Three different batches of 20 medium-size worms of each species were scattered along the soil surface, when they soon burrowed into the soil, and they were left undisturbed for 8 hours. The apparatus was normally left in darkness. At the end of the experiment the number of worms in different sectors along the temperature gradient was counted. The soil

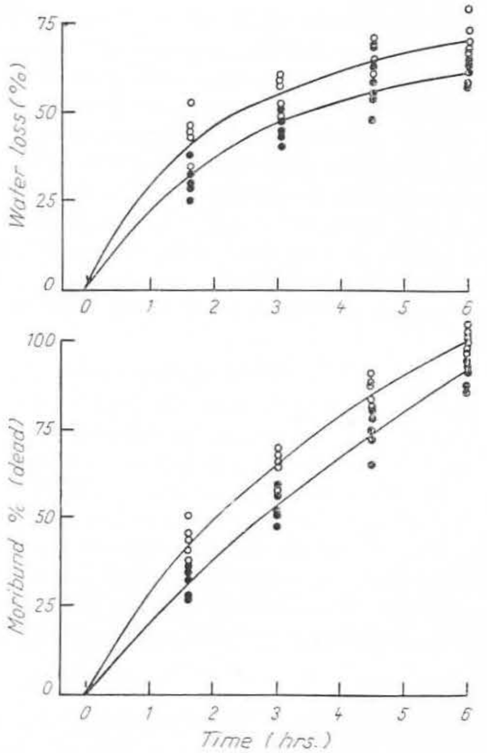

Fig. 10. Mortality and water-loss of eudrilids (dark symbols) and hyperiodrilids (light symbols) in dry air at 25 °C.

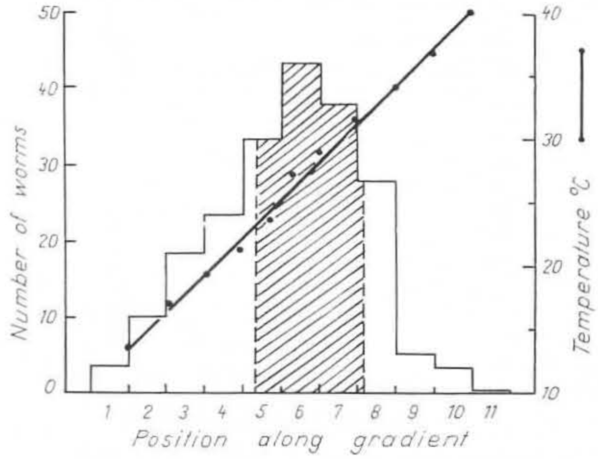

Fig. 11. Effect of a temperature gradient in moist soil (water content: 12.5 %) on the distribution of earthworms. 50 % aggregation (23.0—31.5 °C) shown shaded.

moisture at the warm end of the apparatus fell to about 10% (oven dry weight basis) owing to condensation on the glass roof; that at the cool end remained unchanged.

The results (Fig. 11) showed that 50 % of the total number of worms aggregated between 23.0—31.5 °C (LSD 5 %: 2.55 i. e. 18—36 °C: LSD 1 %: 3.34 i. e. 16—33.5 °C), with a peak at about 28.5 °C. Temperatures above 34 °C were markedly avoided: the distribution in the „cool half“ of the apparatus decreased regularly as the temperature decreased. Worms at the cold end were capable of slow movement.

3.9. Effects of temperature extremes

3.9.1. *High temperatures*

Earthworms of each species were collected from the field, put into aerated tap water for several hours at about 25 °C and then left in plastic boxes lined with moist blotting paper for 48 hours. The worms were then exposed to different constant temperatures by leaving them in 5 m*l* water in test-tubes plugged with cotton wool. The test-tubes were submerged to the neck by lead weights in a metal rack placed in a water-bath, constant to ± 0.1 °C (Cercotherm Mk. II, Shandon Ltd.). This set-up was maintained at the required temperature for about 30 minutes before dropping the worms into the tubes. A total of 20 medium-sized worms of each species was used at each temperature. The first series of experiments lasted for 1 hour and the second series for 12 hours.

Table 6 gives the results. When first dropped into the test-tubes, the worms stopped moving immediately and remained still for the remainder of the experiment. (a) For experiments lasting 1 hour, all the *Hyperiodrilus* and *Eudrilus* specimens remained alive at 36 °C and 37 °C respectively. After 12 hours, all the specimens of both species were alive at 33.5 °C. The worms in both experiments remained alive for at least 2 further days, when they were discarded. (b) Other worms were dead after 1 hour at 38.0 °C and 38.5 °C respectively, and after 12 hours at 34.5 °C for both species. The dead worms were partly autolised after 1 hour and completely so after 12 hours. (c) After 1 hour at 37 °C about half the total number of hyperiodrilids died but all the eudrilids remained alive. At 38 °C *Hyperiodrilus* died, whereas nearly three-quarters of the total number of *Eudrilus* were alive. After 12 hours differences were less apparent, but more eudrilids remained alive at 34 °C.

Table 6. Thermal death point of earthworms, showing numbers remaining alive 2—3 days after experiments at different temperatures. Twenty individuals used for each experiment

Temperature °C	1 hour (n = 20)		12 hours (n = 20)	
	Eudrilids	Hyperiodrilids	Eudrilids	Hyperiodrilids
39.0	0	—	—	—
38.5	0	0	—	—
38.0	14	0	—	—
37.5	19	7	—	—
37.0	20	11	—	—
36.0	20	20	0	0
35.0	20	20	0	0
34.5	—	—	0	0
34.0	—	—	11	6
33.5	—	—	20	20
33.0	—	—	20	20
32.0	—	—	20	20

3.9.2. *Low temperatures*

Batches of 10 medium-sized worms of each species were collected from the field, left in aerated tap water at about 25 °C for several hours and then put in boxes lined with moist blotting paper for 48 hours. The worms were then transferred to cold water in containers left in a refrigerator, kept at 16, 12, 10.7, 8.5 and 7.5 °C (± 1 °C) in separate experiments for 3 hours and then examined.

Observations showed that individuals of both species were active at the three highest temperatures, but became immobile at 8.5 °C. When left in the laboratory the worms previously at 8.5 °C started moving again when the temperature of the water reached 13 °C in 20 minutes. None recovered after 3 hours at 7.5 °C. Hence, the chill coma temperature for both species after 3 hours is 8.5 °C, which is considerably below expected field temperatures in Nigeria (Table 7).

3.10. Effect of hydrogen ion concentration

Different solutions giving a range of *p*H's from 2.0 to 10.0, in 0.4 *p*H units, were prepared using the following solutions: *p*H 2.0—4.0: potassium phthalate and HCl; *p*H 4.4—6.0: potassium phthalate and NaOH; *p*H 6.4—7.2: potassium phosphate and NaOH, and *p*H 7.6—10.0: boric acid and potassium chloride (Cole 1955). Medium-sized worms of each species were collected from the field and left overnight at about 25 °C in aerated distilled water. Each worm in turn was then lightly held around the middle of the body with forceps, and after it had extended, the prostomium and anterior body segments were dipped in *p*H solution. The time taken for the withdrawal of the submerged portion of the body was then recorded. An individual worm was not tested in more than 5 different solutions, and it was returned to distilled water for about one minute before each test. The worm was then replaced in aerated distilled water and not used again until at least 4 hours later. A total of about 50 worms of each species was used, and a minimum of 30 different observations made with each *p*H solution.

Figure 12 summarises the results. Between a *p*H of 2.0—4.0 the worms (both species) invariably contracted instantaneously, and usually remained contracted until replaced in distilled water. At a *p*H of 4.4 the majority of them still contracted; at a *p*H of 4.8 the worms withdrew on about half the occasions. At a *p*H of 5.2 they rarely contracted. In solutions of *p*H's ranging from 5.6—9.2 there were no withdrawals, but the worms in solutions of *p*H 8.4 and above became increasingly agitated. Finally, in *p*H solutions of 9.6 and 10.0, they contracted spasmodically. The optimum *p*H for both species, therefore, falls between 5.6—9.2.

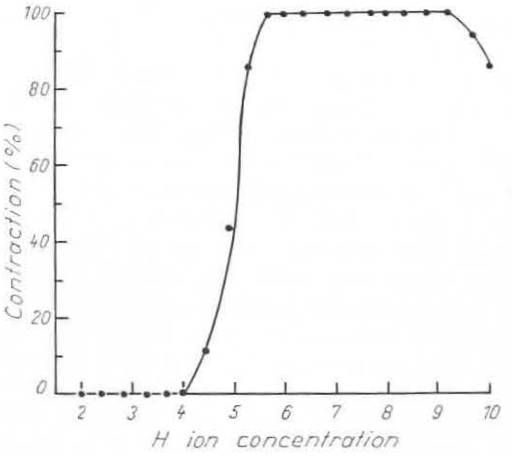

Fig. 12. Behaviour of earthworms in solutions of different hydrogen ion concentrations, at 25 °C.

4. GENERAL DISCUSSION

This work investigates some aspects of the biology of two species of earthworms commonly found in southern Nigeria, West Africa. Field studies were confined to the earthworm population of open and, particularly, shaded grassland on the campus at the University of Ibadan. Ibadan is situated on the border of the semi-deciduous tropical rain forest, with a well-marked wet season from about April-October and well-marked dry season from about November—March. The mean annual rainfall is about 120 cm and the mean annual air temperature ranges from 21—32 °C (MADGE 1965a). This discussion relates present investigations with previous work made on earthworms from temperate and other tropical regions, and correlates laboratory and field results where possible.

In common with other tropical species (GATES 1961) surface casting of the Nigerian earthworms is limited to the wet season. Two types of earthworm casts were clearly evident: one funnel-shaped and confined to shaded, sometimes bare, grassland, and the other mound-shaped and confined to open grassland. The first type of casts was voided by *Hyperiodrilus africanus* BEDDARD and the second by *Eudrilus eugeniae* (KINBERG). Although the mature forms of both these species are small compared with the surface casting European species (ARTHUR 1965), the casts produced by the Nigerian species are considerably more impressive than those voided by earthworms in temperate regions.

Surface casts were not produced during the first 2—3 weeks of the rainy season, although the soil remained permanently moist. Moreover, attempts to maintain casting activity at the start of the dry season or to initiate casting before the wet season began by artificially supplied moisture, were unsuccessful. By contrast, *Lampito mauritii* continued casting during the dry months in Burma in regularly moistened habitats, but other oriental species did not and became inactive before the end of the rainy season. Ten species of lumbricids from Maine, U. S. A., also remained active throughout the year when the soil was kept permanently moist (GATES 1961). However, one of the Nigerian species (*Hyperiodrilus africanus*) found in abundance in soil in low-lying forest in the vicinity of a stream, continued casting for several weeks after the onset of the dry season until the soil eventually dried. Mass migration of earthworms as the soil dried out at the end of the rainy season was not observed, but this phenomenon was common to several earthworm genera in Burma (GATES 1961). Mass immigration of eudrilids from their burrows was frequently noted during daytime on open grassland in response to raiding activities of predatory ants, after which the earthworms were quickly killed and eaten.

Earthworms in temperate regions are active mainly during spring and autumn. Of the 37 known British species of lumbricids, only *A. longa* and *A. nocturna*, and to a lesser extent *L. terrestris*, make well-defined surface casts. Approximate estimations give an earthworm population of 1—3 millions per acre in grassland soils in temperate regions (SATCHELL 1958), weighing 500—1,500 lbs. per acre, and producing an average of 11 tons (range 1—25 tons) of surface casts per acre each year (EVANS 1948). This represents a layer of soil 0.25 cm thick each year. Less information is available on similar data in tropical earthworms. There were about 140 thousand earthworms per acre in a mixed lowland forest at Ibadan (only one collection taken), depositing 90 tons of surface casts per acre per year (MADGE 1965a). NYE (1955) showed that *Hippopera nigeriae* produced 100 tons of surface casts per acre per year in a moist tropical forest in Ghana. Results in the present work indicate that an average of 121.5 thousand individuals of *Hyperiodrilus* per acre in shaded grassland voided over 70 tons of casts each wet season, that is, a soil surface 1.5—2 cm thick will be formed each year, providing that it is not washed away.

Other invertebrates are also responsible for depositing surface soil. Thus, soil turnover by termites in the tropics sometimes approaches that of earthworms. NYE (1955) found that up to 25 termite mounds per acre, each weighing 2.5 tons, were produced by *Macrotermes nigeriensis* BL. CAPS. on the surface of a freshly cleared forest; that is, up to 62.5 tons of soil was thrown up per acre. However, an average of two termite mounds/acre was more common. The organic matter of termite mounds was only slightly greater than that of the surrounding soil (NYE 1955). On grassland at Ibadan, ants voided 0.5—2 tons of surface mounds per acre, consisting largely of sand particles, with a very low organic matter content. By contrast, the organic matter content of earthworm casts was appreciably higher than that of the topsoil, like casts produced by earthworms in temperate regions.

The mechanical composition of the surface casts of both Nigerian species consisted of a fine sandy loam, which was probably ingested at least 100 cm below the surface, mixed with organic matter near the soil surface, and then ejected on to the surface. The topsoil had a higher proportion of coarse sand than other sand fractions, which increased further down the profile, then below about 50 cm changed to a sandy loam again. Although earthworm casts often enrich the surrounding topsoil, in the area investigated they were partly washed away during torrential outbreaks of rain. In temperate regions earthworm casts produced on permanent grassland are more resistant to the disintegrating action of rainfall than those produced on arable soil (SWABY 1950). The contribution of earthworms in modifying the topsoil at Ibadan is less obvious than that observed by NYE (1955) in Ghana, where their activities considerably changed the top soil layer. WATSON (1962) and NYE (1954) fand that termites were also responsible for modifying different soil horizons in East and West Africa respectively.

Regular weekly sampling throughout the wet season in shaded grassland at Ibadan recovered hyperiodrilids in all stages of development. When placed into different size-groups, it became clear that there was probably one generation of earthworms at the start of the rainy season and a second generation near the end of it. Because worms at the onset of the wet season were mostly mature and those at the end of the wet season were mostly small, it appeared that worms did not diapause or aestivate during the dry season, but continued their development further down the soil profile where it was moist. Laboratory experiments showed that in constant moist soil, and at a temperature approximating to that of the soil in shaded grassland during the dry season, a third generation was obtained which corresponded in time to the middle of the dry season. Unfortunately, too few earthworm cocoons were found to corroborate these observations.

Little information is available on the life-history of other tropical earthworms. In the monsoon tropical climate of Burma, rainfall controls the life cycle of earthworms (Gates 1961). Breeding in most species was generally limited to the last 1—2 months of the rainy season, one generation a year being usually produced. Also, in North India, with a humid sub-tropical climate, endemic species had a breeding cycle either late during the wet season or one throughout the year. Gates (1961) states that some tropical species probably have two generations each year, but this was not confirmed in the laboratory. Mud-inhabiting species and other worms in permanently moist sites, however, remained uninfluenced by the seasons and continued breeding throughout the year.

More is known about the life-cycles of earthworms in temperate regions, where both temperature and moisture control their seasonal activities. Field populations show spring and autumn peaks. The cocoons of 11 species of earthworms had incubation periods varying from 10—21 weeks when deposited from mid-August to mid-May (Evans and McL. Guild 1948b). The main surface casting species, *A. longa* and *A. nocturna*, reproduced from mid-March to mid-July and again from October to November, with an obligatory diapause during the summer. The reproductive activities of 6 other species of lumbricids were interrupted between March and December (Evans and McL. Guild 1948a).

Laboratory investigations were also made on the behaviour of the Nigerian earthworms to various controlled physical conditions. Whenever possible, results of laboratory experiments are correlated with observations made in the field, and results also compared with those of other workers. Since there were no obvious differences in behaviour in laboratory experiments between either species of earthworm, only combined results are usually given.

In a gradient of soil with different moisture contents ranging from 1 to 23% (oven dry weight) earthworms moved towards and remained in soil with 12.5—17.2% moisture. However, the optimum soil water content selected by the worms is not related to their surface casting activity, for in another experiment, they casted mainly in soil with a moisture content of 15.8—28.0%. This may explain why surface casts were not observed following the first few showers of the rainy season, although a few worms were collected from the soil; the worms probably became active only when optimal soil moisture conditions were reached for casting. Other work has shown that the majority of individuals of *Pheretima hupeinsis* and half the total number of *A. caliginosa* aggregated mainly in the highest soil moisture in a gradient of 14.5—30.1% of sandy, loamy soil, although generally a gradient of 20—30% was selected. None moved towards soil containing 18% moisture or less (Grant 1955a).

In common with worms from temperate regions, both Nigerian species survived for long periods in soil in aerated tap water. Roots (1956) found that six common species of British lumbricids survived for $2^1/_2$—$5^1/_2$ months at 8—18 °C. Most of the Nigerian species survived for at least 2 months under similar conditions, but at 25 °C. Feeding was not evident, the worms showing little or no increase in size during this period and the gut, through the translucent body wall, appeared empty. This was unexpected, for their life-history is rapid and hence fast development of individuals would be expected. In the laboratory, however, worms without food died in under a month, as did those in experiments by Roots (1956). When *L. terrestris* and *A. caliginosa* were offered an alternative choice of either water or damp blotting paper, the first species avoided the water and the second chose either. However, when initially acclimatized to water, both species chose water. Also, cocoons of both species developed under water, produced worms, which fed and developed, but did not reproduce under water (Roots 1956). *P. hupeinsis* and *E. foetida* were more active on wet than on dry surfaces, but *A. caliginosa* was inactive on both surfaces (Grant 1955a).

In a gradient of different sand fractions from 1.0 to 0.1 mm in diameter, the Nigerian earthworms aggregated mainly in sand particles of 0.25 mm in diameter, where they formed surface casts. A mechanical analysis of surface casts from the soil in which they were recovered showed that nearly half of the total sand fractions consisted of fine sand (0.2—0.02 mm diameter).

Several species of European earthworms belonging to the genera *Allolobophora* and *Lumbricus* will show a facultative diapause in slowly drying soil under natural conditions (Michon 1949; Saussey 1963, 1960a and b). The worms empty their gut, become coiled inside earthworm capsules lined with mucous, and remain inactive until the soil is wetted, when the dispause is then often broken. Such earthworms will not diapause in moist soil. Hence, diapause appears to have a survival value which prevents excessive water-loss under adverse conditions. Other earthworms do not diapause but avoid desiccation by penetrating deep down into moist soil. In the laboratory, both species of Nigerian earthworms did not appear to diapause in drying soil, but moved downwards in advance of the drying front, where they eventually became desiccated, remained extended and died. Field observations during the dry season also failed to recover any worms in diapause. Gates (1961) observed tropical earthworms in tightly clustered aggregations in moist soil near the water table during the dry season. The significance of these aggregations in moist soil is obscure.

In common with species of earthworms in temperate regions (Jackson 1926, Grant 1955a; Roots 1956), the water-content of *Hyperiodrilus* (88.4 %) and *Eudrilus* (83.8 %) fell within the limits of 75—90 % (oven dry weight). The Nigerian worms all died in dry air after 6 and $7^{1}/_{4}$ hours respectively, unlike desiccated *L. terrestris*, which all died in $2^{1}/_{2}$ hours (Hogben and Kirk 1944). The Nigerian species showed no dehydration syndrome, as did *L. terrestris* (Wolf 1938a). These earthworms lost less weight in dry air after 50 % mortality compared with temperate earthworms, and hence appeared to be more resistant to desiccation. For example, *P. hupeinsis*, *A. caliginosa* and *E. foetidus* lost 48.6, 58.8 and 63.4 % body weight respectively; *Eudrilus* and *Hyperiodrilus* lost 43.3 and 45.0 % respectively. The greater resistance of *Eudrilus* to desiccation and its longer survival in dry air compared with *Hyperiodrilus* is probably of some adaptive value, for the soil in which eudrilids live is liable to dry out more rapidly than that inhabited by hyperiodrilids.

Like the majority of poikilotherms, earthworms select a temperature optimum in a temperature gradient in uniformly moist soil. Thus, Smith (1902) using crude methods, found that *E. foetidus* showed little response in temperatures of 20—29 °C, avoided 30—35 °C, and died in temperatures of 35—40 °C. Grant (1955b) using a soil temperature gradient of 0.8—75 °C for 24 hours, recovered *P. hupeinsis* mainly at 15—23 °C, *E. foetida* at 15.7—23.2 °C and *A. caliginosa* at 10—23.2 °C. Laverack (1961b) showed that the central nervous system of *L. terrestris* gave a steady rate of nervous impulses in a temperature range of 5—22 °C, with an optimum at 13—17 °C, suggesting that this species was most active in the field at these temperatures. Both species of tropical earthworms aggregated mainly in moist soil at 23—31.5 °C, with a peak at about 28.5 °C. Thus, they appeared to be adapted to a higher temperature optimum than earthworms in temperate soils. The worms markedly avoided temperatures above 34 °C, and tolerated, but with a decreasing bias, temperatures from 23 to 13 °C. These results may be compared with the average daily temperatures of grassland soil at different depths during the year (Table 7). There was a remarkably small range in soil temperature variation throughout the year, with an average annual difference of about 6 °C at 5 cm depth and less

Table 7. Average monthly soil temperature at different depths in grassland soil for 1964 at Ibadan, Nigeria. Rainfall also included

Month	No. rainy days	Total rainfall (mm)	Temperature °C 5 cm	10 cm	20 cm	30 cm	120 cm
January	1	3.0	28.8 (24.4—32.8)	28.8 (26.7—32.2)	28.9 (27.8—30.0)	28.3	28.9
February	1	0.9	32.4 (26.1—38.9)	32.2 (28.3—36.1)	31.0 (30.0—32.2)	30.5	29.4
March	7	81.8	**32.7** (26.7—38.9)	**32.5** (28.9—36.1)	**31.1** (30.6—32.8)	**30.6**	**30.6**
April	16	203.8*)	31.0 (26.1—32.8)	30.9 (27.8—33.9)	30.3 (28.9—31.7)	29.4	30.0
May	14	189.5	29.7 (25.0—31.1)	30.0 (27.2—32.8)	29.4 (27.8—30.6)	28.9	29.4
June	19	159.7	31.4 (24.4—32.2)	28.6 (26.7—30.0)	28.9 (27.8—30.0)	28.3	29.4
July	23	386.7	26.7 (23.7—29.4)	27.5 (25.6—29.4)	27.6 (26.7—28.3)	27.2	28.3
August	22	199.0	**26.4** (23.3—29.4)	**27.0** (25.0—28.9)	**26.7** (25.0—28.9)	**26.7**	**27.2**
September	11	118.5	27.4 (24.4—30.6)	27.8 (25.6—30.0)	27.5 (26.7—28.3)	27.2	27.3
October	10	83.4	29.6 (24.4—35.0)	29.3 (25.6—30.0)	27.5 (26.7—27.8)	28.3	28.3
November	5	33.3	29.6 (25.0—34.4)	29.6 (26.7—32.8)	28.6 (27.2—30.0)	28.3	28.9
December	0	0	29.6 (25.0—34.4)	29.6 (26.7—32.2)	28.6 (27.8—29.4)	29.4	28.9

Note — Soil temperatures averaged from four different readings at 0700, 1000, 1600 and 1800 hrs. local time. Range in brackets. Rainfall taken from standard rain gauge, 12.5 cm in diameter, 4.5 m above ground level.

*) Rainfall in April above average.

than 4 °C at 120 cm depth. The difference in diurnal temperature, however, was greater, with a daily variation at 5 cm depth of about 7 °C during the wet season and about 11 °C during the dry season, and at 20 cm depth of 2—3 °C during both wet and dry seasons. The peak temperature optimum of the worms coincided with the average annual temperature in the soil profile. The average soil temperature at different depths during the dry season fell within the upper temperature optimum of the worms, although variations in day temperature suggested that the temperature was generally too high for them to produce surface casts, even if the soil was artificially watered. However, during the wet season the daily temperature fluctuations suggest that surface casting was possible, even during daytime, and this sometimes occurred after rainfall on dull, humid days. The field temperature was never below that of the lower limit of the preferred temperature of the worms in laboratory experiments.

Laboratory experiments were also made on the survival limits of both species of Nigerian earthworms to high and low temperatures. The upper thermal limit of other worms have been found by several workers, but owing to different acclimatisation periods, lengths of exposure and criteria used to express mortality, comparisons are difficult. Earthworms may take at least two weeks to become acclimatized to a particular temperature. Thus, Grant (1955b) found *P. hupeinsis* required 12 days to become acclimatized to an increase in temperature from 15 to 22 °C. When worms were kept at 4, 9 and 15 °C for one month, the upper thermal limits were 19.4, 20.9 and 22.9 °C respectively. Grant (1955b) concluded that with this species there was an average gain of heat tolerance of 0.3 °C for every 1 °C increase in acclimatization temperature. Although some earthworms apparently require relatively long periods for acclimatization, Rogers and Lewis (1914, 1916) noted that *L. terrestris* reached thermal equilibrium in water in about 2 minutes. Smith (1902) found that *E. foetida* died in a temperature range of 35—40 °C, but the length of exposure to these temperatures and pre-conditioning are not stated. When *L. terrestris* was acclimatized at 10 °C half the total number of the worms died when left for $6^{3}/_{4}$ hours at 28.5 °C (Wolf 1938b). Above 29 °C the worms all died. In these experiments, both the front and hind ends of the worms had similar temperature thresholds. Hogben and Kirk (1944), however, found that the upper thermal limit of this species was 29.0 ± 0.5 °C for 12 hours exposure. In moist air in temperatures above the upper thermal limit, the body temperature was about 2 °C higher than the wet bulb temperature, providing that the latter was 7 °C below the air temperature; in relatively dry air the difference was about 5 °C (Hogben and Kirk 1944). Grant (1955b) acclimatized worms at 22 °C then determined 50 % mortality for 48 hours at different temperatures. The upper thermal limits for *P. hupeinsis* was 24.9 °C, and for *E. foetidus* and *A. caliginosa* 24.7 °C each. Miles (1963) kept worms in soil at 15 °C for at least 4 weeks and then found their 80 % survival rates after 12 hours exposure. The upper thermal limit for *E. foetidus* was 33.3 °C and for *A. longa* 25.7 °C. The first species was thus adapted for surviving the relatively high temperatures of its natural environment in compost heaps, and the second species adapted for aestivating in deeper soil in hot, dry weather (Miles 1963). The upper survival limits of both Nigerian species of earthworms after 1 or 12 hours were appreciably higher than those of temperate species, which thus enable the tropical species to withstand the relatively high temperatures of their environment. Although there is a small temperature difference in the upper thermal limits between *Hyperiodrilus* and *Eudrilus*, suggesting a slight adaptation to a shaded and sun-exposed environment respectively, these small adaptive differences are probably of little significance in the soil. Differences in behaviour between the two species in the soil are probably more important than adaptation to high temperature.

Investigations have also been made on the lower thermal limits of earthworms, although more information is available for high temperature. Schmidt (1918) found that *A. foetida* failed to recover after exposure to temperatures below —1.6 to — 2.0 °C, and stated that the range of temperature permitting life for this species was —2 to 28 °C. *L. terrestris* remained alive in water at 2 °C after 1 hour and in melting ice for longer than 12 hours (Hogben and Kirk 1944). Grant (1955b) found that at 3 °C *E. foetida* died in less than 5 days, *P. hupeinsis* lived for 7 days and *A. caliginosa* survived for several weeks. Both Nigerian species survived for 3 hours but became immobilized at 8.5 °C, and none survived at 7.5 °C. These temperatures are considerably below those liable to be found in their environments (Table 7), and hence are of no adaptive importance. The results obtained with the temperate species, however, suggest an adaptive tolerance to the low winter temperature of their environment (Dowdy 1944).

Field investigations have shown that earthworms can be divided into three groups: acid tolerant, acid intolerant and ubiquitous species. In the laboratory, earthworms are sensitive to differences in hydrogen ion concentration, and will show marked aversion to sub-optimal *p*H solutions. For instance, Satchell (1955) found that 5 common species of British earthworms violently avoided *p*H solutions of 2.2—2.6 but remained quiescent in *p*H solutions of 3.0—5.8, with intermediate reactions at a *p*H of 2.8. When left in soils with a range of different H ion concentrations, they remained on the soil surface with a *p*H of 4.0, and eventually died or became partly buried in soil with a *p*H of 4.4 and actively burrowed into different soils with a *p*H of 5.0—7.0. By recording electrical changes of the nervous system, Laverack (1961a) found acid-sensitive fibres on all areas of the earthworm's body surface, including the prostomium. Threshold responses reflected differences in the field distribution of the worms. Thus, the nervous system of *A. longa*, *L. terrestris* and *L. rubellus* responded mainly to a H ion concentration of 4.4—4.6, 4.1—4.3 and 3.8 respectively. In nature, these worms are not usually found in soils with a *p*H of less than 4.5, 4.2 and 3.7 respectively. The behaviour of both species of Nigerian earthworms also varied markedly in solutions with different H ion concentrations. A *p*H range of 2.0—4.0 was violently rejected, a *p*H range of 5.6—9.2 was accepted, and reactions to a *p*H of 4.4—4.8 and 9.6—10.0 were intermediate. Hence, both the tropical species withstood a wide range of H ion concentrations, but the worms are appreciably more acid intolerant than the British species. In the present investigations, both species were collected from soil with a variation in H ion concentration from 7.5 in the topsoil to 5.8 at 100 cm depth (Table 4). Since the H ion concentration decreased regularly down the profile and reached near-optimum conditions at 100 cm depth, it is thus possible that the worms were unlikely to be found much below this depth, with increasing acidity. The *p*H of the surface casts of 7.5 is near the middle of the optimum *p*H range (*p*H 5.6—9.2) in laboratory experiments.

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5. SUMMARY

(1) Investigations were made on the activities of tropical earthworms found in grassland soil in Nigeria, West Africa.

(2) Two main species were found, *Hyperiodrilus africanus* Beddard and *Eudrilus eugeniae* (Kinberg), confined to soil in shaded and open grassland respectively.

(3) *Hyperiodrilus* produced funnel-shaped surface casts and *Eudrilus* mound-shaped casts.

(4) About 70 tons of surface casts/acre/year are produced by each species.

(5) Casting was limited to the wet season, lasting from May—October. Worms did not cast on artificially moistened soil, either before or after the wet season.

(6) There are probably two generations of hyperiodrilids during the wet season. Laboratory experiments indicated that a third generation is also probably produced during the dry season, deeper in the soil where it remains moist.

(7) The topsoil was modified by the activities of both species of worms.

(8) Using both species, it was concluded from laboratory experiments (at 25 °C) that

(a) in soil with a moisture gradient earthworms aggregated in soil with a moisture content of 12.5 and 17.2 %, but casted mainly in soil with a moisture content of 18.5 and 28.0 %;

(b) they survived in mud in aerated tap water for over two months, but died in aerated tap water without mud;

(c) in a gradient of different sized sand particles, the worms aggregated mainly in sand with particles of 0.25 mm in diameter and casted;

(d) in slowly drying soil there was no diapause or aestivation, but the worms became desiccated and died;

(e) when desiccated in dry air, *Hyperiodrilus* all died after 6 hours and lost 69.4 % of their original body-weight; *Eudrilus* all died after $7^{1}/_{4}$ hours and lost 62.3 % of their original body-weight. The water-content of the worms was 88.4 and 83.8 % respectively;

(f) in uniformly moist soil with a temperature gradient of 13—40 °C, the majority of the worms aggregated between 23—31.5 °C, with a peak at 28.5 °C;

(g) the upper thermal limit of *Hyperiodrilus* and *Eudrilus* for 1 hours in water was 37.5 and 38 °C respectively, and for 12 hours it was 34 °C for both species. The lower thermal limit for 3 hours was 8.5 °C, and both species died at 7.5 °C; and

(h) in solutions of different H ion concentrations ranging from a *p*H of 2.0—10.0, in 0.4 *p*H units, the worms contracted violently in a *p*H of 2.0—4.0, and remained quiescent in a *p*H of 5.6—9.2. Reactions to other *p*H solutions were intermediate.

There were no obvious differences in behaviour between either species in most of the laboratory investigations.

(9) A general discussion is given, relating present investigations with others made on earthworms in temperate and other tropical regions, and indicating adaptive differences. Laboratory and field investigations are also correlated where possible.

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Address of the author: Dr. DAVID S. MADGE, Department of Biological Sciences, Wye College (University of London), Ashford, Kent, England.